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**CARBON DIOXIDE AND WATER EXCHANGE OF A SOYBEAN STAND
GROWN IN THE BIOMASS PRODUCTION CHAMBER**

PREPARED BY:	Dr. Kenneth A. Corey
ACADEMIC RANK:	Associate Professor
UNIVERSITY AND DEPARTMENT:	University of Massachusetts Department of Plant & Soil Sciences
NASA/KSC	
DIVISION:	Biomedical Operations and Research
BRANCH:	Life Sciences Research Office
NASA COLLEAGUE:	Mr. John Sager
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ABSTRACT

Soybean (*Glycine max* l. Merr. cv. McCall) plants were grown under metal halide lamps in NASA's Biomass Production Chamber. Experiments were conducted to determine whole stand rates of carbon dioxide exchange and transpiration as influenced by time of day, CO₂ conc, irradiance, and temperature. Plants were grown at a population of 24 plants/m², a daily cycle of 12 hour light/12 hour dark, an average temperature regime of 26 C light/20 C dark, and a CO₂ conc enriched and maintained at 1000 ppm during the photoperiod.

A distinct diurnal pattern in the rate of stand transpiration was measured at both ambient and enriched (1000 ppm) conc of CO₂. Transpiration rates declined during the photoperiod, dropped to about 30 % of maximum in the dark, and then increased during the dark period. Water loss increased by a factor of 1.2 when CO₂ was reduced to the ambient level (about 370 ppm). No distinct diurnal rhythm in CER was measured suggesting that rates of NP obtained from early photoperiod drawdowns of CO₂ are representative for characterizing carbon assimilation during growth and development of a soybean stand. Carbon dioxide did not saturate photosynthesis in the range of conc used (up to 1200 ppm). Whole stand CCP values of 66 and 85 ppm were measured at 2 developmental stages.

CER increased linearly with increasing irradiance up to the maximum attainable with the MH lamp source (500 to 550 $\mu\text{mol}/\text{m}^2/\text{s}$). LCP values for the whole stand were in the range of 76 to 105 $\mu\text{mol}/\text{m}^2/\text{s}$; an increase occurring with increased stand age presumably attributable to an increased background rate of respiration. Temperature had marked effects on stand CER and transpiration rates. NP increased with temperature from 22 to 26 C but then decreased when the temperature was set at 30 C. DPR increased with increasing temperature. Net carbon assimilation was highest when temperature regimes of 26 C light/18 C dark or 22 C light/22 C dark were used. Water flux increased with increasing VPD, the driving force governed by the saturation vapor pressure of the intercellular leaf spaces.

Data generated in this study represent true whole stand responses to key developmental and environmental variables and will be valuable in database construction for future working CELSS. Crop growth studies in the BPC have been conducted with a high degree of environmental control, gas tightness during growth, and have used large plant stands. These characteristics have placed it in a unique position internationally as a research tool and as a pre-prototype subcomponent to a fully integrated CELSS.

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LIST OF ABBREVIATIONS AND ACRONYMS

BPC	Biomass Production Chamber
CER	Carbon dioxide Exchange Rate
CCP	Carbon dioxide Compensation Point
CELSS	Controlled Ecological Life Support System
conc	concentration
DPR	Dark Period Respiration
HPS	High Pressure Sodium
LCP	Light Compensation Point
MH	Metal Halide
NA	Net Assimilation
NP	Net Photosynthesis
PAR	Photosynthetically Active Radiation
PPF	Photosynthetic Photon Flux
ppm	parts per million
RH	Relative Humidity
VPD	Vapor Pressure Deficit

I. INTRODUCTION

The Biomass Production Chamber (BPC) at NASA's Kennedy Space Center is currently a one-of-a-kind plant growth chamber being used as a pre-prototype to a controlled ecological life support system (CELSS). Economically important crop plants are being grown under the semi-closed conditions of the BPC in order to test growth responses to the unique designs and environmental control subsystems developed for the chamber (1,2,3,4). Thus far, complete production grow-outs of wheat (Triticum aestivum), leaf lettuce (Lactuca sativus), and soybean (Glycine max L. Merr.) have been conducted in the BPC.

In comparison to studies in conventional growth chambers, the high degree of environmental control and the large size of the enclosed plant stand combine to provide the BPC with the advantage of a well-integrated sample (5). The BPC has been designed and constructed to be operated as a closed, nearly gas-tight system which enables real time measurements of changes in gas composition throughout growth and development. As a large cuvette, the BPC is extremely "tight"; leak rates in the presence of partial pressure gradients of carbon dioxide have been measured to be in the range of 0.08 to 0.42 % per hour (2; Drese 1989, unpublished data). Such leak rates would have negligible effects on short term determinations of gas exchange rates, particularly those involving the monitoring of changes in atmospheric gas concentrations as influenced by environmental variables.

Rather than relying upon numerous instantaneous measurements of single leaf or single plant measurements to estimate large stand responses, very rapid and reliable rate determinations can be made directly on entire stands. Whole stand measurements avoid the disadvantage of selecting representative sample locations on individual plants for instantaneous rate measurements. The degree of closure of the BPC which has increased for each successive growout conducted is also important for evaluating the performance of crop plants in an environment where trace gas emissions such as ethylene may build up to levels which affect growth and development.

Previous work with wheat (4,5) and soybean (Wheeler, unpublished) has demonstrated that carbon dioxide exchange rates of whole stands are comparable to those obtained from single leaf measurements. With the ratio of plant material to chamber volume and planting configurations used for BPC crop growth experiments, the plant stand responds similarly to single leaves. A notable exception is the light compensation point. Whole stands

typically have light compensation points which are 3 to 5 fold higher than those determined on single leaves (5,6,7).

In this study, a second complete growth and development dataset with soybean as a test crop will be constructed with emphasis on whole stand gas exchange. In the first growout, high pressure sodium lamps were used. The second study will utilize metal halide lamps which provide for lower irradiance but increased spectral emission in the 400 to 500 nm waveband. The study will thus enable a comparison of growth and yield components under the two light sources.

Specific objectives of this study were to determine the rates of gas exchange (CO_2 , O_2 , and H_2O) of a soybean stand in response to stage of development, light, CO_2 concentration, and temperature under the semi-closed conditions of the BPC.

II. MATERIALS AND METHODS

2.1 PRODUCTION DETAILS

On May 5, 1990 soybean (cultivar McCall) seed imbibed for 24 hours in a 2.5 mM $\text{Ca}(\text{NO}_3)_2$ solution were sown in the BPC at the rate of 12 seeds per 0.25 m^2 tray and later thinned to provide a stand of 6 plants/tray or 24 plants/ m^2 . Environmental conditions in the BPC were as follows: a 12 hour light/12 hour dark daily regime was used, light was provided with metal halide lamps, temperature was set at 26 C for the first 2 days and then a light/dark regime of 26/20 was used after 2 days except when temperature was used as an experimental variable, relative humidity was maintained at 85 % for the first 4 days after planting and then at 65 to 70 % for the remainder of growth, and carbon dioxide concentration was maintained at a setpoint of 1000 ppm during the photoperiod following drawdown to that concentration after the dark respiration period.

As a second growout of soybean in the BPC, most other cultural practices and conditions were the same as the first except that high pressure sodium vapor (HPS) lamps were used in the first. The metal halide (MH) lamps used in this study provided for a lower irradiance at full power (500 to 550 $\mu\text{mol}/\text{m}^2/\text{s}$ after 4 weeks growth) than the HPS lamps. At 100 % power to the lamps the output of the MH lamps in PAR was about 75 % of the HPS lamp output (Wheeler, unpublished data). However, the MH lamps provide considerably greater emissions in the blue waveband (400 to 500 nm) previously shown to reduce internode length and overall stem elongation of soybean (8).

Additional detail on production techniques including the composition of the nutrient solution, system configurations, and manipulations can be found in Wheeler et al. (9).

2.2 GAS EXCHANGE RATE CALCULATIONS

Rates of net photosynthesis (NP) and dark period respiration (DPR) were calculated daily by computing the slopes of the lines fit by linear regression from the changes in CO_2 concentration occurring in the BPC atmosphere following the transitions from lights on and off (Figure 1). Since the dark period respiration led to a CO_2 conc in excess of the 1000 ppm setpoint and no scrubbing device was used, it continued to increase throughout the entire 12 hour dark period. Data points from the first 15 to 30 minutes following a lights on or off transition were not used because there were concomitant changes in temperature which led to changes in the pressure of the BPC atmosphere. These pressure events were transient, but enough to cause mass flow of gases into or out of the BPC depending upon the direction of the total pressure gradient (into the BPC when temperature was decreased). For DPR rates, data from the remainder of the period was used and for NP rates data up to the first injection of CO_2 was used. Calculations were based on a chamber volume of 112,060 liters and a growth area of 20 m^2 . Application of the ideal gas law was made to correct the volume for different temperatures used for light and dark periods and for temperature experiments.

Oxygen concentration in the BPC atmosphere was monitored with a S-3A Oxygen Analyzer (Ametek, Thermox Instruments Division, Pittsburgh, PA) which uses a solid oxide (stabilized zirconia) sensor cell. This sensor provides for readings to within $\pm 0.02\%$ O_2 . Since very small changes in oxygen were being measured in a large background concentration (i.e. 20.8 %), detection sensitivity was insufficient to be used for reliable short term rate calculations. However, trends were observable and are presented to show a typical diurnal pattern (Figure 1).

Transpiration rates were calculated by measuring the total volume of condensate collected over a given time interval. Rates are expressed in $\text{mmol H}_2\text{O}/\text{m}^2/\text{s}$.

2.3 DIURNAL GAS EXCHANGE RATES

Two experiments were conducted to determine if diurnal rhythms in the rates of CO_2 and H_2O exchange exist. For CER, rates from the dark period increase, beginning of photoperiod drawdown, and mass additions over 3-hour time increments were obtained. For transpiration rates, condensate tanks were emptied and the volume

of water measured at 3-hour intervals. The first experiment was conducted 50 days after planting. In the second experiment, the same measurements were made at two CO₂ conc. After the first day at the standard enriched level of 1000 ppm, CO₂ was brought down to the ambient conc (about 370 ppm) 2 hours prior to the dark period. Except for the early photoperiod drawdown following increases due to DPR, CO₂ was maintained at a setpoint of 350 ppm.

2.4 EFFECTS OF ENVIRONMENTAL VARIABLES ON GAS EXCHANGE RATES

2.4.1 EFFECT OF IRRADIANCE

On days 23, 33, and 54 irradiance from the MH lamps was varied to provide 5 levels and a dark treatment. Settings for dimming the light banks were made on the programmable logic controller and adjusted to provide for approximately uniform treatment for the range of irradiances used, since there was considerable variation in the actual output of individual lamps for a given dimming setting. At the start of the experiment, the conc of CO₂ in the BPC was raised to approximately 1600 ppm and each irradiance level maintained for 1-hour segments. Slopes of the changes in CO₂ versus time were obtained from 40-min segments in the middle of each 1-hour treatment. Actual irradiances incident at approximately the top of the canopy for each treatment were measured either immediately following the experiment or the day following the experiment with a sunfleck ceptometer (model SF-40, Decagon Devices Inc., Pullman, WA 99163). Irradiance was measured as a photosynthetic photon flux (PPF), i.e. in the photosynthetically active wavelength region of 400 to 700 nm. Irradiance was measured over each of the 64 growth trays at days 23 and 33. At 54 days, the canopy had developed to the extent that fencing was required for support. Small openings were made in the fencing for tray positions 2, 6, 10, and 14 at each level and incident PPF readings taken at the canopy top over the 4 trays on each level.

2.4.2 EFFECT OF CARBON DIOXIDE CONCENTRATION

On days 24 and 56, the automated control of the 1000 ppm CO₂ setpoint was manually overridden and the CO₂ conc allowed to drawdown to the compensation point. Almost the complete photoperiod was required to achieve this and just prior to the dark period, the CO₂ conc was raised back to the 1000 ppm setpoint. Carbon dioxide exchange rates were determined before, during, and after the drawdowns.

2.4.3 EFFECT OF TEMPERATURE

Temperature setpoints for the light/dark portions of the daily cycle were varied in two separate experiments to provide for 3 different temperatures for each half of the daily cycle. In the first experiment, the light/dark temperature regimes were as follows: 22/18 (day 35), 26/22 (day 36), and 30/26 (day 37). In the second experiment, the order was varied and light/dark regimes were 26/18, 22/22, 26/26, and 30/22 (days 41-44). All temperature and relative humidity readings logged during the different regimes were retrieved and averages across the 4 levels and all times calculated. The actual temperatures and relative humidity values were used to calculate a vapor pressure deficit (VPD) which is the water vapor gradient between the intercellular spaces of the leaf and the BPC atmosphere. The intercellular spaces were assumed to be at saturation. Therefore, the VPD was calculated as the difference between the saturation vapor pressure at a given temperature and the actual vapor pressure (obtained from the product of the relative humidity and the saturation vapor pressure).

III. RESULTS AND DISCUSSION

3.1 DIURNAL GAS EXCHANGE RATES

The CO₂ exchange rate during the photoperiod 50 days after planting was between 25 and 30 $\mu\text{mol}/\text{m}^2/\text{s}$ (Figure 2). The first point was acquired from early photoperiod CO₂ drawdown data while the subsequent 3 points were calculated from mass additions of CO₂. In general, photosynthetic rates calculated from mass additions were 1.12 (standard deviation=0.22; N=47) times higher than those calculated from the drawdowns. It was not determined whether the CER data in Figure 2 is attributable to a distinct diurnal rhythm or if in fact there are inherent differences in the values obtained by the different calculation methods. The mass flow method of calculation should provide a slight overestimate of NP due to the chamber leak rate, but not to the extent of 0.12. Evidence for a diurnal rhythm in stomatal conductance has been obtained (10) and in this experiment there was a distinct decrease in the quantity of condensate collected during the photoperiod, suggesting that stomatal conductance decreases toward the end of the day. However, this daily pattern in stomatal conductance may not affect the CER.

During the dark period, the respiration rate remained relatively constant, but there was a distinct increase in the transpiration rate. Initially, the transpiration rate in the dark was about

one-third of that which occurred at the beginning of the photoperiod. Nevertheless, this represents a substantial rate of water loss during a period when most plants under field conditions have greatly diminished stomatal conductances (7). The data suggest a fairly clear diurnal pattern of transpiration presumably controlled by a rhythm in the degree of stomatal aperture. There does not, however, appear to be as much of an effect of this rhythm on CER, which is in agreement with previous findings in a growth chamber study (10).

Daily measurements of NP and DPR enabled a continuous tracking of gas exchange with growth and development (Figure 3). After 3 weeks from planting the stand was developed sufficiently to observe distinct patterns of CO_2 conc increases and decreases due to DPR and NP, respectively. The rate of NP increased from 15 $\text{umol/m}^2/\text{s}$ at 3 weeks to about 25 $\text{umol/m}^2/\text{s}$ after 4 weeks at which time it leveled off. Following pod set and during the early stages of pod fill, the rate of NP declined slowly (after 50 days). The rate of DPR also increased early in development, but not to as great an extent as the rate of NP. Since each portion of the daily cycle was 12 hours in duration, the net assimilation of CO_2 was simply calculated by difference. The lack of smoothness in the data is explained by light, CO_2 drawdown, and temperature experiments conducted at various times throughout development. Following the collection of a complete data set through harvest, the data will be processed to develop a carbon mass budget and to determine if net assimilation can be interpreted and used as a biomass predictor. In general, absolute values for CER determined on whole soybean stands and expressed on a m^2 basis compare within a factor of 1 to 2 of those measured on single leaves and plants (11,12,13).

3.2 IRRADIANCE

Within the range of irradiances tested (0 to 517 $\text{umol/m}^2/\text{s}$), CER was related linearly to PPF indicating that light was well below saturation for the stand density and temperatures used (Figure 4). The light compensation points (LCP) as with wheat stands (5) were substantially higher than those measured on single leaves. The LCP values in this study were less than those obtained from the previous growout with HPS lamps. Perhaps there is more efficient utilization of the PAR emitted from the MH lamp source due to differences in both intensity and spectral quality. Some plants have been shown to shift their LCP's in response to decreased irradiance as a part of an 'acclimitization' process (14).

A 36 % increase in the LCP occurred between day 33 and day 54. This may be attributed to a greater background respiration as measured in the dark. While DPR is not the same as respiration occurring in the light, it provides an estimate of the magnitude of CO₂ evolution in the light and does provide an explanation for the increase in LCP with increased stand age (see also Figure 3).

3.3 CARBON DIOXIDE

A total photosynthetic drawdown of CO₂ preceded and followed by DPR increases 24 days after planting is illustrated in Figure 5. Prior to the drawdown, DPR was relatively constant throughout the 12 hours. Following the drawdown DPR was considerably less than that which occurred before the drawdown and a change in slope occurred during the last one-third of the dark period. The rate of DPR before the drawdown was 1.73 times the rate following the drawdown, suggesting that the available pool of carbohydrate was depleted by bringing the CO₂ conc down to near the compensation point (about 66 ppm). The increase in DPR during the latter stages of the dark period was suggestive of a mobilization/metabolism of reserves.

When the same experiment was conducted 56 days after planting the ratio of DPR rates before and after the drawdown was only 1.26. At this stage of development, the absolute DPR rates were 1.5 to 2 times higher than at 24 days. The question is why the stand did not appear to be as carbohydrate depleted by the CO₂ drawdown later in development. Perhaps at this stage of development, the soybean plants are exporting carbohydrate from the leaves to developing pods and converting it into storage compounds (i.e. protein and lipids) at a rapid rate, developing pods contribute more to stand respiration than the leaves, and low free carbohydrate pools affect the rate of pod respiration very little.

Data obtained from the CO₂ drawdowns also enabled the calculation of CER as a function of CO₂ conc. Data at approximately 30 minute intervals were extracted from the entire drawdown data set and slopes calculated between adjacent time points and converted into rates of NP. Data from the day 24 and 56 drawdowns are illustrated in Figure 6. Carbon dioxide compensation points for the 2 drawdowns were about 66 and 85 ppm, respectively. These values are somewhat higher than the CCP measured for wheat (5) and those reported for other C-3 plants (6,7). In the BPC, there is a high rate of air movement (about 4 chamber exchanges/min) and therefore development of boundary layers of gases is probably minimal except deep within a dense canopy. Perhaps the lag in CO₂ diffusion from the root mass resulting from respiratory

activity through the tray covers led to higher CCP values for a whole stand than those measured on leaves or single plants.

In the range of 400 to 500 ppm there was a sharp change in the CER. Over the entire range of CO₂ conc used, NP is apparently not quite saturated as indicated by the slightly positive slope occurring after about 500 ppm. The generation of dose-response relationships such as this for whole crop stands will provide valuable input data for functioning CELSS.

The CER at enriched CO₂ averaged 1.4 times that which occurred at ambient levels (Figure 7). The same general pattern of CO₂ exchange as the previous diurnal experiment (Figure 2) was observed over the 4-day experiment except for the first day at the ambient level. Reduction of CO₂ to ambient conc caused a 1.2 fold increase in the transpiration rate in the light but had no effect on water loss in the dark. This is in agreement with previous findings (15,16) and with the known effect of CO₂ on stomatal conductance (increased CO₂ results in decreased stomatal conductance). As with CER, a diurnal pattern of transpiration similar to that obtained in the 1-day diurnal experiment at the enriched CO₂ was observed.

3.4 TEMPERATURE

In the range of 35 to 37 days after planting the rate of NP was affected little by a temperature increase from 22 to 26 C but decreased by 1.8 $\mu\text{mol}/\text{m}^2/\text{s}$ when increased from 26 to 30 C (Figure 8). Rates of DPR increased progressively with increasing temperature which led to a decrease in the net assimilation of CO₂ with increasing temperatures used for the light/dark periods. A comparison of the 2 common temperatures for NP and DPR (22 and 26 C) shows that there would be no difference in the net assimilation (0.85 $\text{mol}/\text{m}^2/\text{day}$) in this temperature range. However, this assumes that there is no affect of the order of temperature episodes, which may not hold true.

In a second temperature experiment (42 to 45 days after planting), a comparison of 2 temperature regimes was made with the two common temperatures for NP and DPR used within a 24-hour period. Net assimilation was highest when the 26/18 and 22/22 regimes were used (0.91 and 0.88 $\text{mol}/\text{m}^2/\text{day}$). In contrast to the first experiment, net assimilation decreased by 0.1 $\text{mol}/\text{m}^2/\text{day}$ when temperature was increased from 22 to 26 C, attributable to both a decline in NP and an increase in DPR. This represents more than a 10 % drop in net carbon fixed. Possible explanations for the disparity in results of CER between the 2 experiments are 1) the later stage of development of the second

experiment was characterized by a larger number of shade senescent leaves which were more sensitive to the increased temperature, and 2) the order in which the temperature episodes are applied had an affect on the rates.

In a working CELSS, temperature regimes will presumably be used to maximize the rate of net assimilation and therefore the biomass production per unit time. However, at times it may be necessary to manipulate temperature regimes to modulate (slowdown or accelerate) the rates of gas exchange within the system to accomodate mass and energy needs and demands.

The temperature experiments also enabled computation of water fluxes for different water potential gradients (VPD). The VPD varied at different temperatures despite fairly rigid control of ambient RH in the BPC because the saturation vapor pressure of water in the intercellular spaces of the plant tissues was assumed to vary. It was assumed that the leaf and other plant tissue temperatures were in equilibrium with the air temperature. Transpiration rate increased linearly with increasing VPD in the light and in the dark (Figure 10). Data points in Figure 10 are from both temperature experiments. This data enables computation of water regeneration capacity under a range of working conditions for a CELSS and as with carbon dioxide exchange may be used to perform manipulations to accomodate or anticipate needs in a CELSS.

IV. CONCLUDING REMARKS

Database construction for crop plants selected for CELSS continued with soybean as a test crop. Whole stand rates of carbon dioxide and water exchange were measured throughout growth and development and as affected by time during a daily cycle, carbon dioxide conc, irradiance, and temperature. As a research cuvette, the BPC is providing whole stand reponses which are currently unrivaled with regard to the degree of environmental control, low gas leakage rate, and large plant sample size. Responses to key environmental variables enable selection of optimum conditions for a CELSS and permit some degree of predictive ability for suboptimum conditions for plants when alterations in growth rates might be dictated by practical considerations such as changing mass and energy availabilities or demands. While many of the responses measured in this study corroborate trends and processes established from classical whole crop physiology studies of the past, the data obtained using the BPC have enabled a higher degree of confidence in the absolute numbers gathered, particularly as they characterize how a large

plant canopy responds. Compared to studies on single leaves and plants, the whole stand gas exchange studies have led to values for carbon dioxide compensation points, light compensation points, and dark transpiration rates generally higher than those reported previously. The gas exchange database gathered using the BPC will also enable mass budget analyses not previously possible with other growth chambers.

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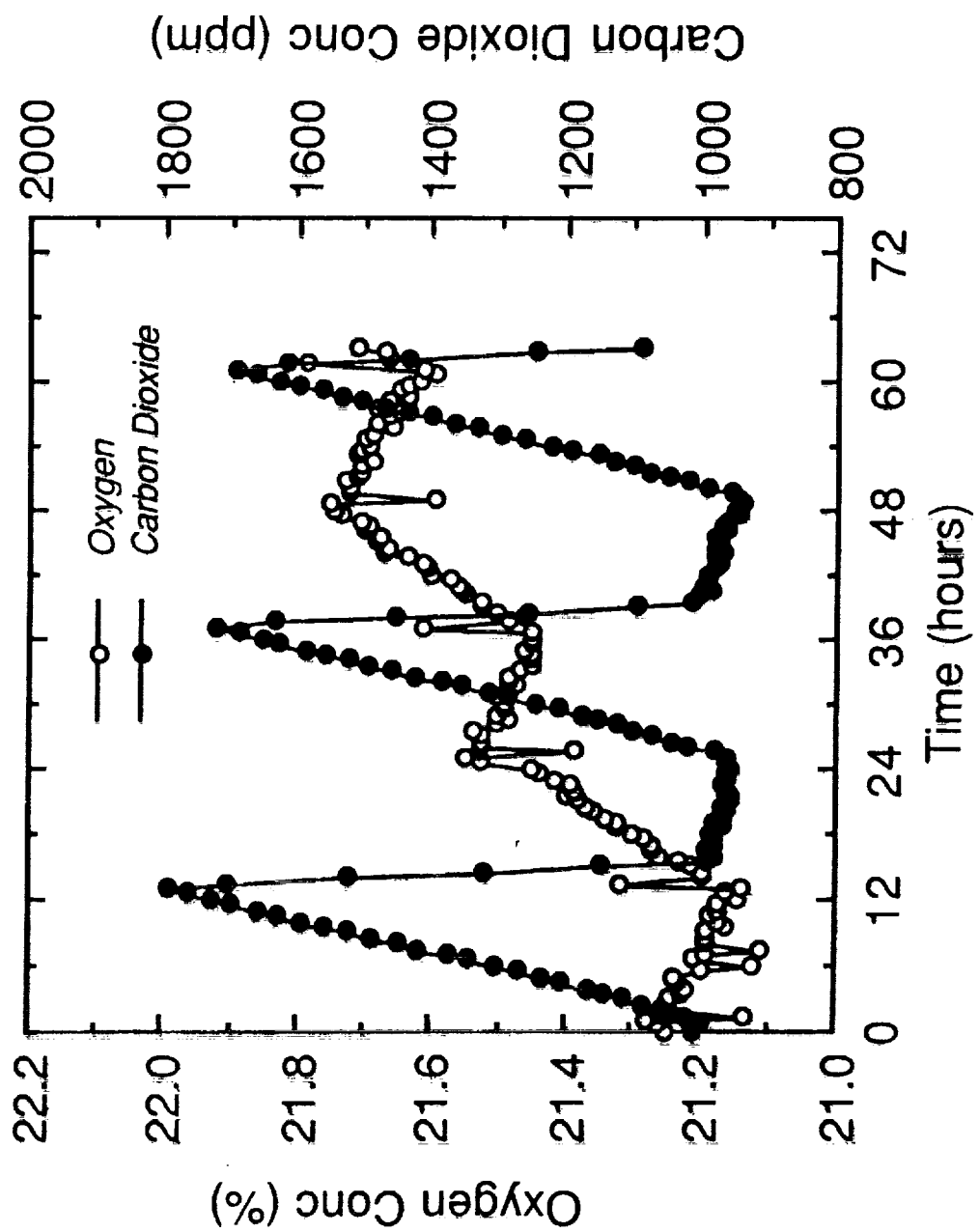


Figure 1

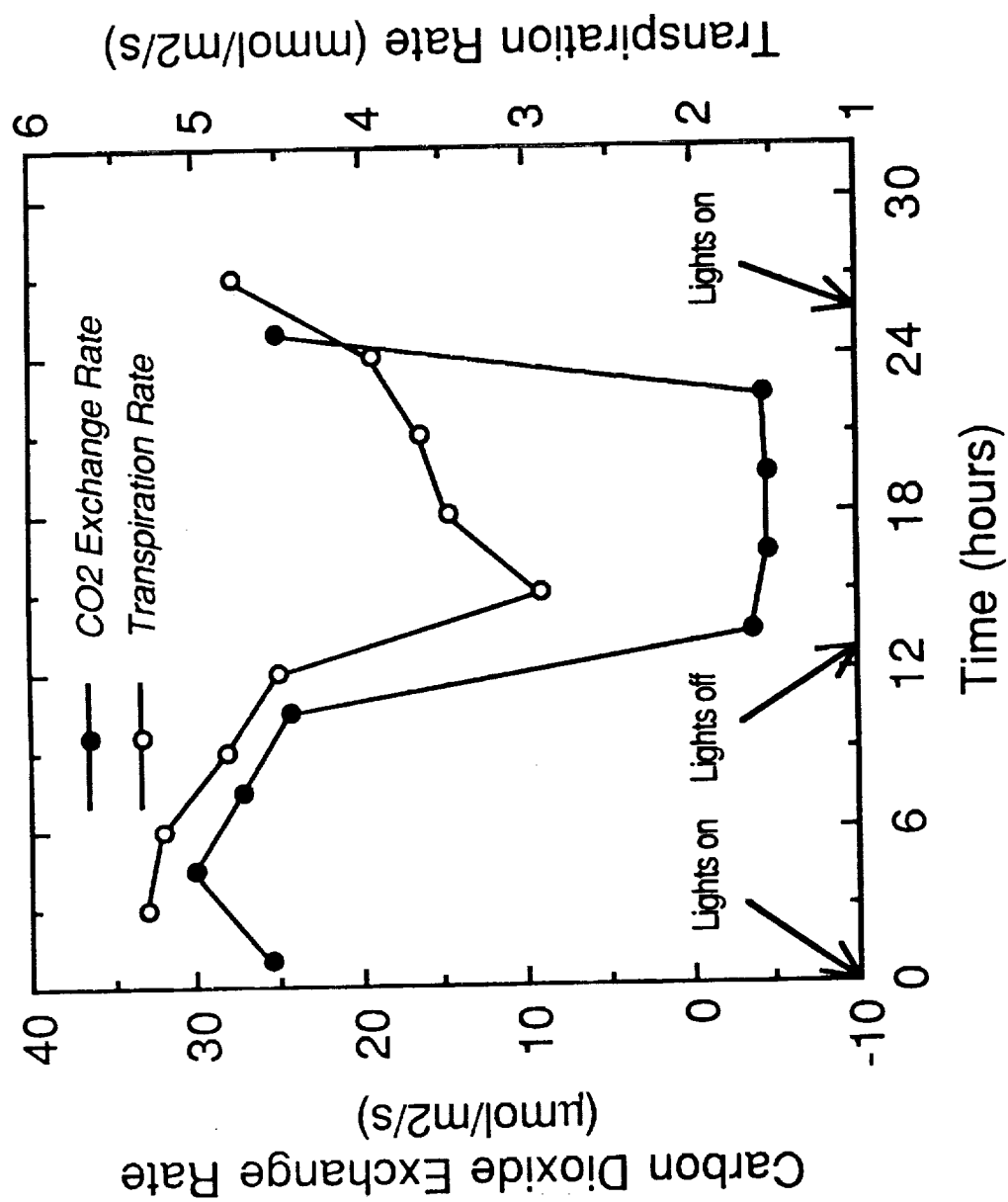
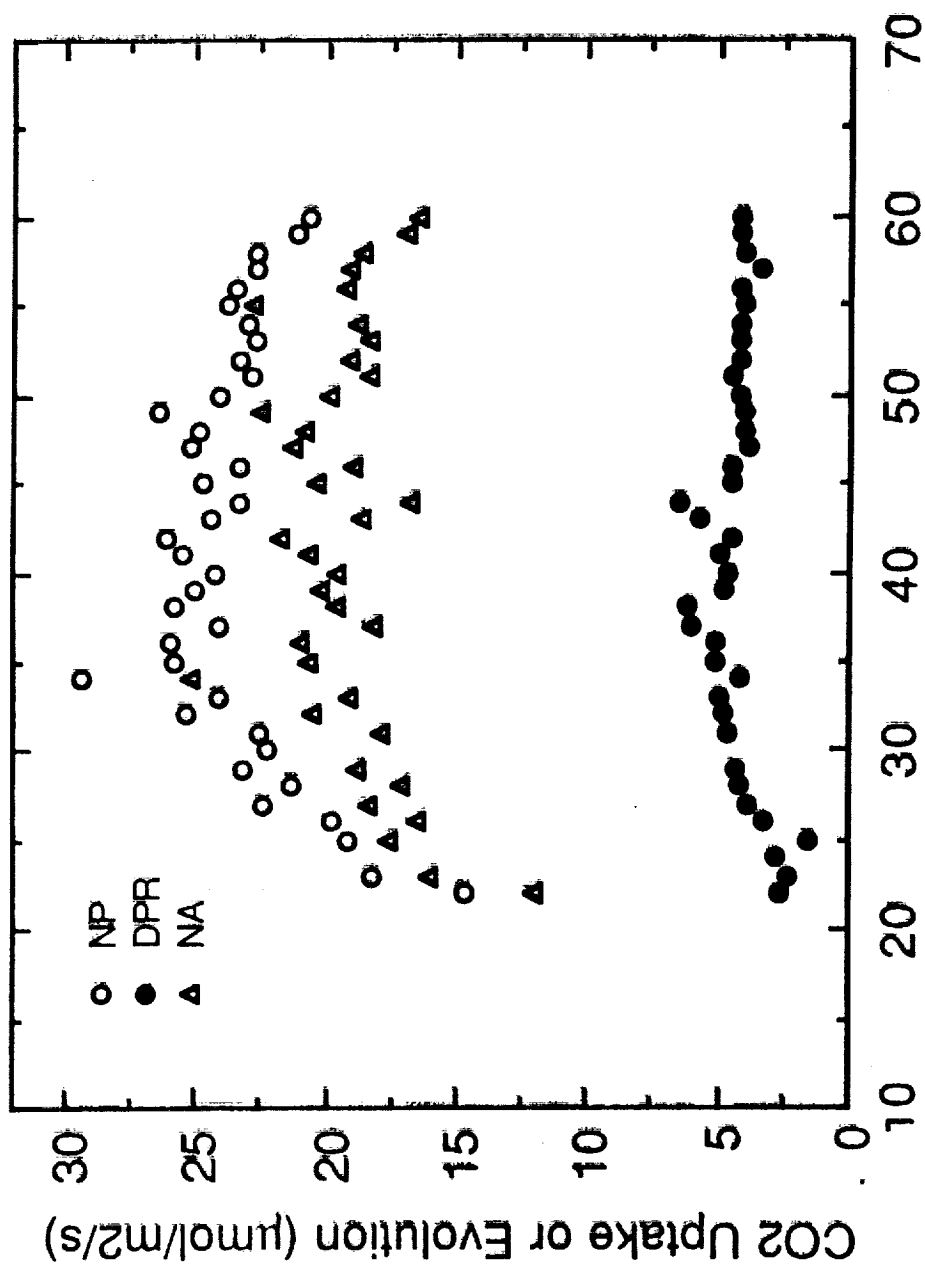


Figure 2



Days After Planting
Figure 3

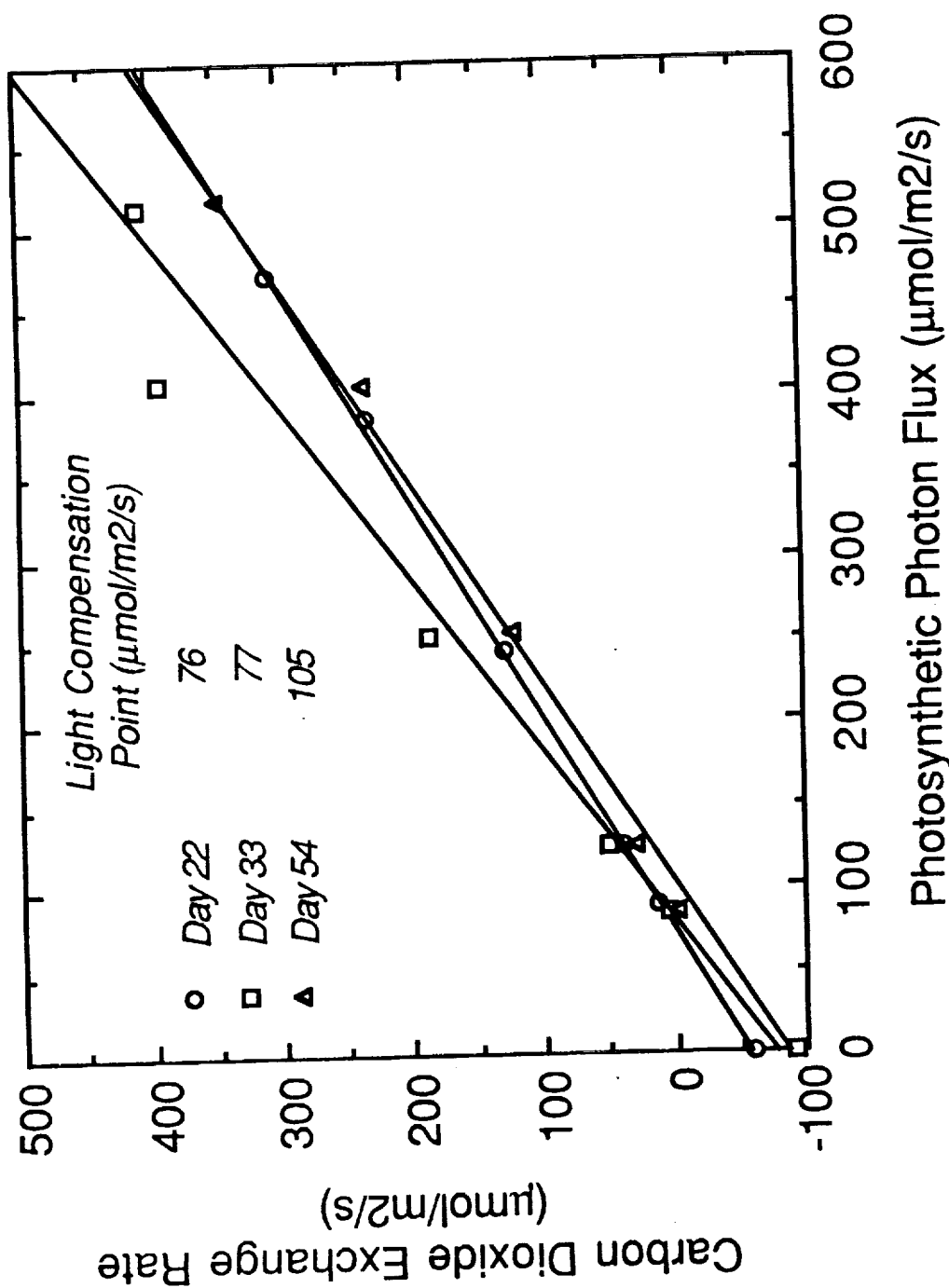


Figure 4

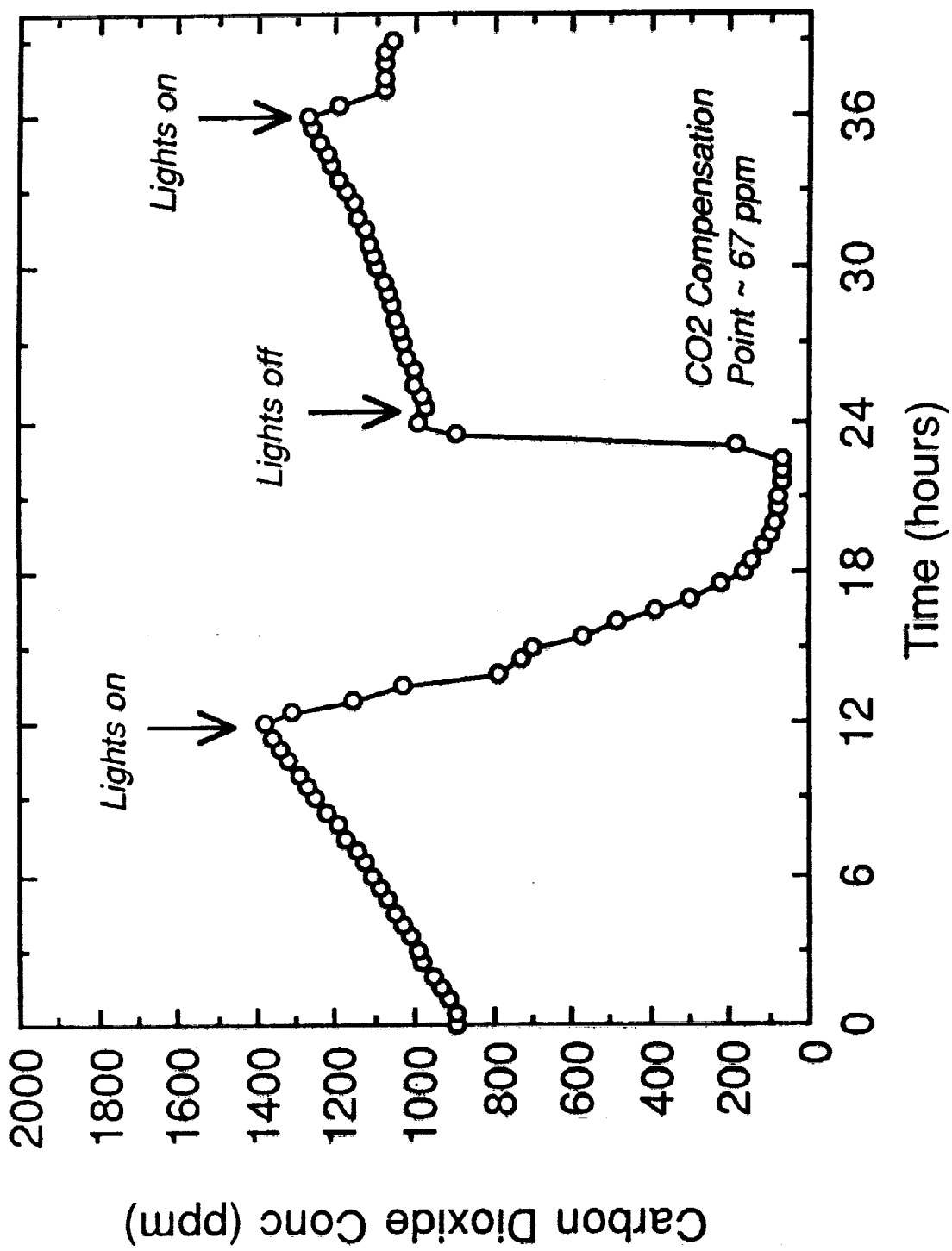


Figure 5

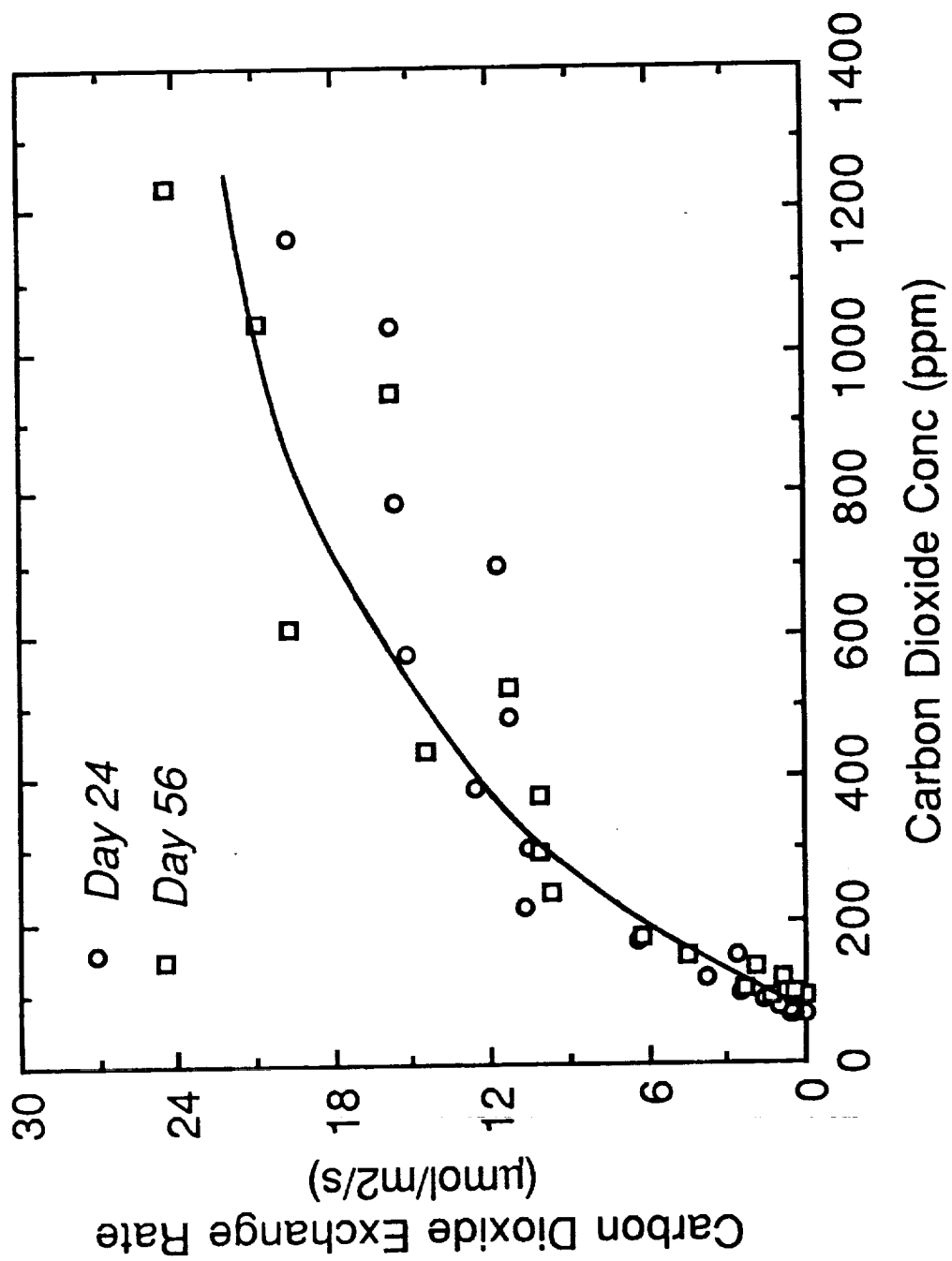


Figure 6

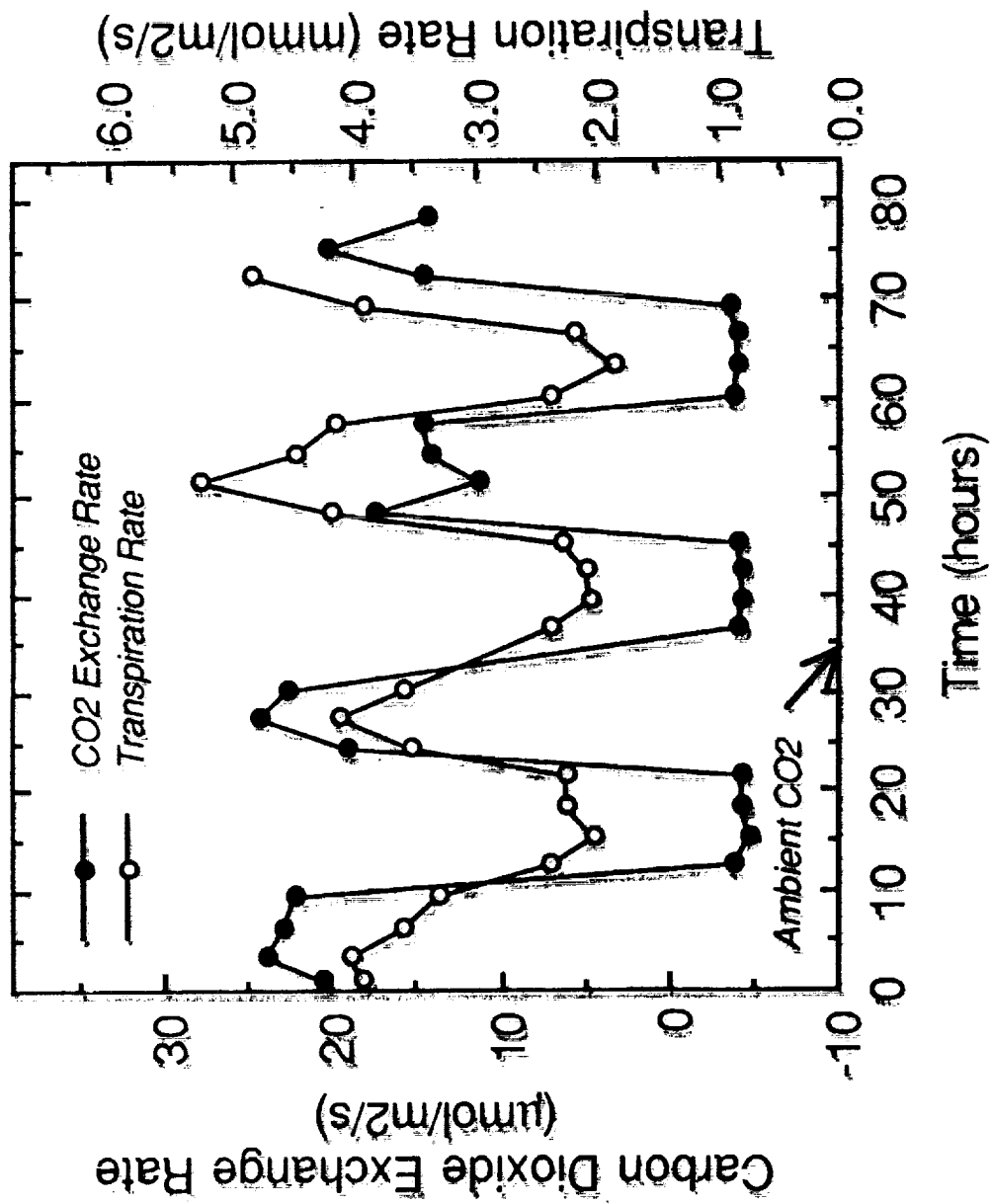


Figure 7

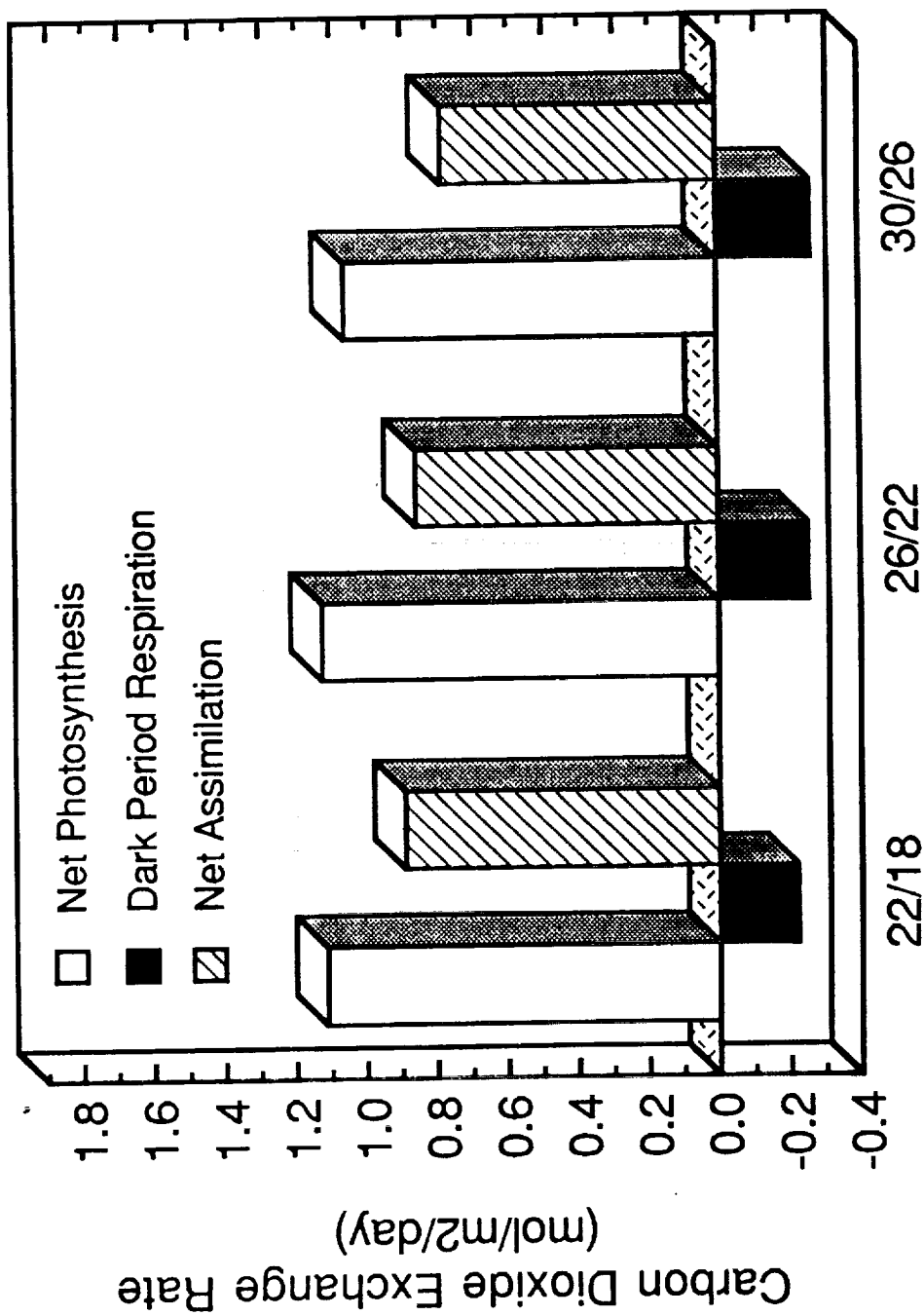


Figure 8
Temperature Regime (Light/Dark)

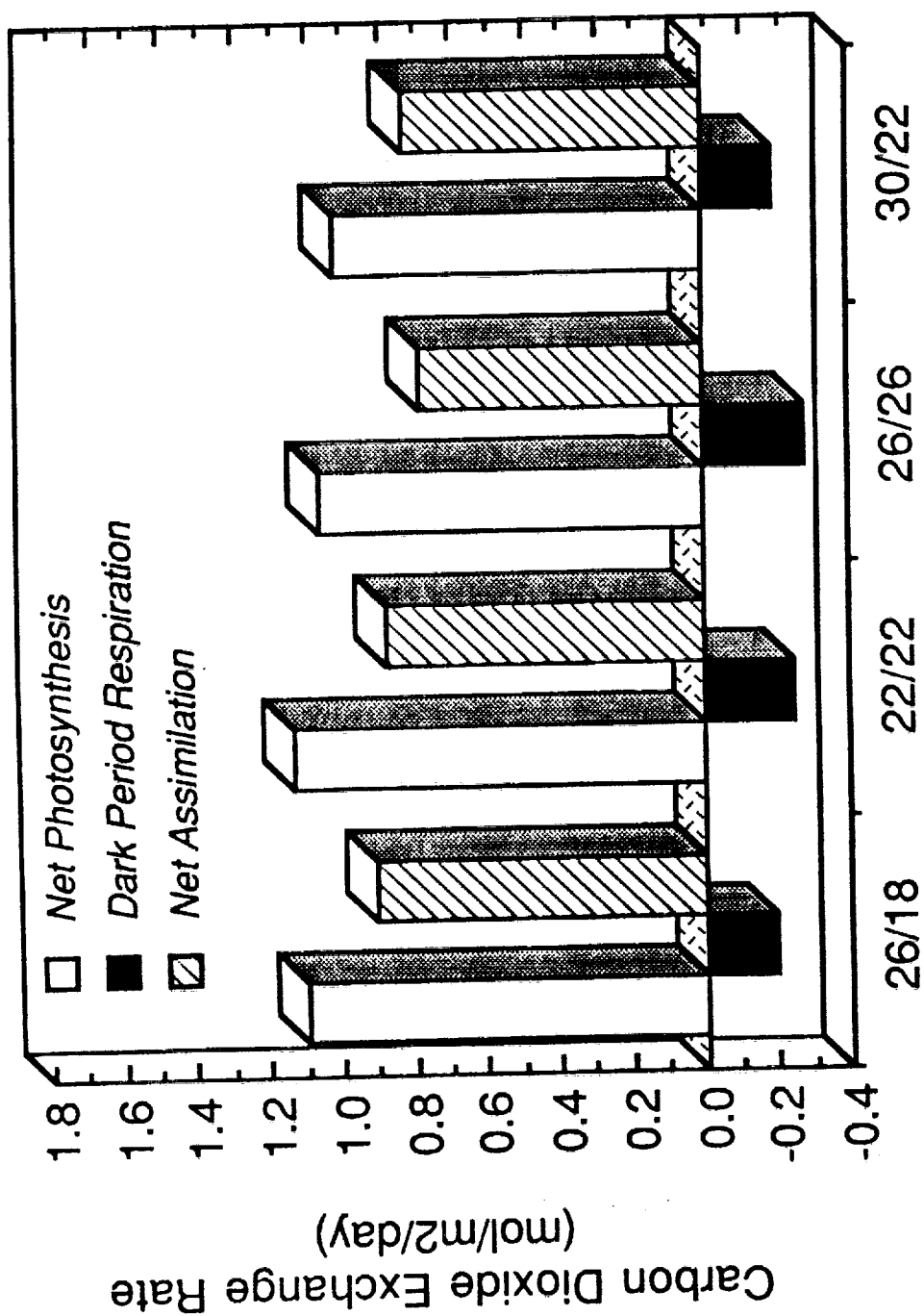


Figure 9
Temperature Regime (Light/Dark)

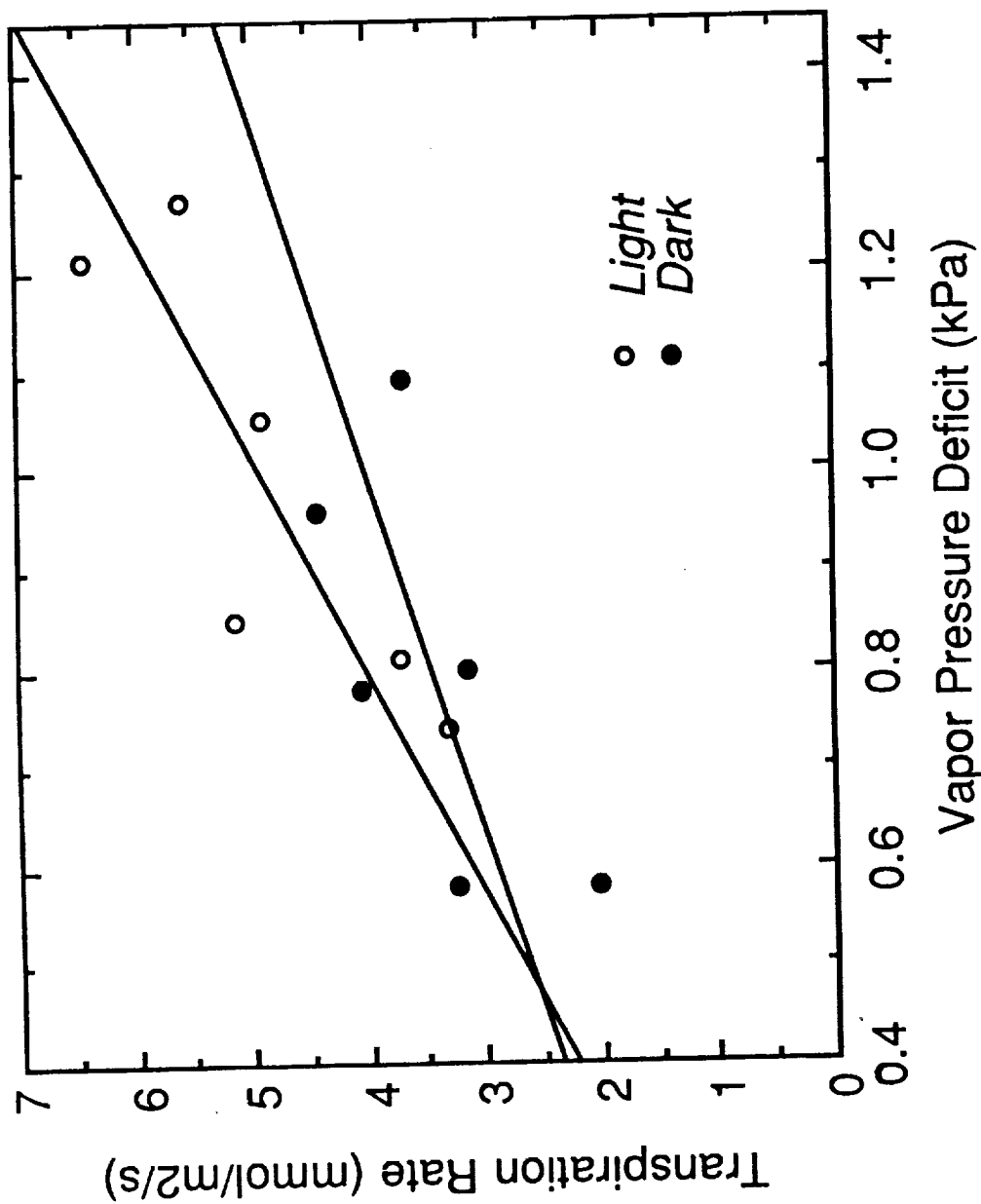


Figure 10